

SPATIALLY-EXPLICIT MODELS FOR INFERENCE ABOUT DENSITY IN UNMARKED POPULATIONS

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Recently-developed spatial capture-recapture (SCR) methods represent a major advance over traditional capture-capture methods because they yield explicit estimates of animal *density* instead of population size within an unknown area, and they account for heterogeneity in capture probability arising from the juxtaposition of individuals and sample locations. Although the utility of SCR methods is gaining recognition, the requirement that all individuals can be uniquely identified excludes their use in many contexts. In this paper, we develop models for situations in which individual recognition is not possible, thereby allowing SCR methods to be applied in studies of unmarked or partially-marked populations. The data required for our model are spatially-referenced counts made on one or more sample occasions at a collection of closely-spaced sample units such that individuals can be encountered at multiple locations. Our approach utilizes the spatial correlation in counts as information about the location of individual activity centers, which enables estimation of density and distance-related heterogeneity in detection. Camera-traps, hair snares, track plates, sound recordings, and even point counts can yield spatially-correlated count data, and thus our model is widely applicable. A simulation study demonstrated that while the posterior distribution of abundance or density is strongly skewed in small samples, the posterior mode is an accurate point estimator as long as the trap spacing is not too large relative to scale parameter (σ) of the detection function. Marking a subset of the population can lead to substantial reductions in posterior skew and increased posterior precision. We also fit the model to point count data collected on the northern parula (*Parula americana*), and obtained a density estimate (posterior mode) of 0.38 (95% CI: 0.19, 1.64) birds/ha. Our paper challenges sampling and analytical conventions by demonstrating that neither spatial independence nor individual recognition is needed to estimate population density — rather, spatial dependence induced by design can be informative about individual distribution and density.

Keywords and phrases: Abundance estimation, camera traps, data augmentation, hierarchical models, N -mixture model, Neyman-Scott process, Poisson cluster process, point counts, spatial capture-recapture, spatial point process, population density, R package unmarked

1. Introduction. Estimates of population density are required in basic and applied ecological research, but are difficult to obtain for many species, including some of the most critically endangered. A primary obstacle faced when estimating population density is that the number of individuals captured or detected is an unknown fraction of the actual number present, N . Capture-recapture (CR) methods yield estimates of N ; however, the effective area sampled, A_e is typically unknown, and thus density cannot be estimated (Dice, 1938; Wilson and Anderson, 1985). This is a well-known deficiency of traditional CR methods that limits their utility for making inferences beyond the indefinite region in which the sampling was conducted.

The limitations of traditional CR methods extend beyond their inability to estimate density. For example, even if A_e were known, CR estimators can be biased by heterogeneity in capture probability resulting from unmodeled spatial variables. In particular, it is intuitive that individuals close to a trap are more likely to be captured than individuals further away. So-called spatial capture-recapture (SCR) models (Efford, 2004; Borchers and Efford, 2008; Royle and Young, 2008; Royle et al., 2009; Gardner, Royle and Wegan, 2009; Borchers, 2010) address these problems and produce direct estimates of density or population size for explicit spatial regions. This is accomplished by modeling the number and locations of individual activity centers as well as distance-related heterogeneity in capture probability. Information about activity centers comes from the spatial coordinates of the traps where individuals were captured — data which have always been available but were rarely utilized until recently.

Because SCR models overcome the limitations of CR methods without requiring additional data, they represent a major advance in efforts to estimate population density, and their use is becoming widespread. However, use of such methods requires that all individuals are uniquely identifiable, which can be difficult to achieve in practice. In some cases, such as in point counts of birds, it is typically not even possible to identify individuals. In other cases, even when resources are available to obtain individual recognition, the identity of many individuals often remains unknown. For example, in “camera trapping” studies (O’Connell, Nichols and Karanth, 2010), the resulting photographs are not always sufficient for identification due to similar markings among animals. In many other cases, no natural markings are present to aid recognition (*e.g.*, fishers, mountain lions, deer), and capturing all individuals encountered may be too difficult or intrusive.

In this paper, we present a model allowing for inference about density and population size *when individuals cannot be uniquely identified*. Our model exploits the spatial structure in observed counts induced by the spatial or-

ganization of count locations that are in close proximity to one another. The key to our approach is, rather than viewing the spatial correlation as an inferential obstacle, we utilize spatial correlation as direct information about spatial distribution and population size. We formulate the model in terms of a collection of latent trap- and individual-specific encounter frequencies and provide a Bayesian analysis of the model based on Markov chain Monte Carlo (MCMC). We demonstrate efficacy of the approach using a simulation study. The model is also applied to a bird survey data set collected on a 50-m grid of 105 point count locations.

Our paper challenges two ingrained and preeminent paradigms in statistical ecology: First is that sample units should be structured so as to ensure independence of the observable random variable¹ and second is that individual information is needed to obtain estimates of population size and density². Our proposed class of models directly refutes both of these paradigms and suggests whole new classes of sampling designs and statistical models for making inferences about animal demographic parameters.

2. Sampling Design. We consider a sampling design in which R traps are operated on T occasions within a region \mathcal{S} , which for simplicity we treat as two-dimensional, $\mathcal{S} \subset \mathbb{R}^2$. Although we use the term “trap”, anything capable of recording counts of unmarked individuals could be used, such as a camera or a human observer conducting a point count, *i.e.*, a survey from a fixed point in space. The sample occasion can be an arbitrary time period, such as a single day in a camera trap study, or a 10-min survey interval. Trap locations are characterized by the coordinates of each trap, $\mathbf{x}_r = (x_{r1}, x_{r2})$; $r = 1, 2, \dots, R$. The data resulting from this design are the $R \times T$ matrix of counts, n_{rt} ; $t = 1, 2, \dots, T$.

Unlike similar count-based sampling protocols, this design aims to induce *correlation* in the neighboring counts by organizing the trap locations sufficiently close together so that individual animals might be encountered at multiple locations. Thus, we do not make the customary assumptions that counts can be viewed as *i.i.d.* outcomes and that no movement occurs between sampling occasions. In the following section we develop a hierarchical model that describes the process by which such correlation is generated.

3. The Hierarchical Model and Data. To devise an inference framework for the observed counts, we specify a hierarchical model consisting of component models for the underlying ecological state process, which in the

¹Hurlbert (1984) has been cited >5000 times according to Google scholar

²Even classical distance sampling relies on sampling of *unique* individuals where identity is equated to a point in space

present case are the activity centers of N individuals, and then a separate model component describing the process of encountering individuals at each trap.

3.1. State model. Suppose that N individuals occur within \mathcal{S} and each individual has an associated activity center around which movements occur. For many species, this could be the center of a home range or a territory. We adopt a pragmatic definition of home range to be the space about which an individual moves during a specific time period (in our case, the interval from $t = 1$ to $t = T$). Denote the coordinates of this activity center $\mathbf{s}_i = (s_{i1}, s_{i2}); i = 1, 2, \dots, N$. Since the activity centers cannot be directly observed, they are regarded as latent variables, which we model as outcomes of a spatial point process. In principle, general point process models could be considered, but here we model activity centers as

$$\mathbf{s}_i \sim \text{Uniform}(\mathcal{S})$$

which is equivalent to assuming

$$s_{i1} \sim \text{Uniform}(0, B)$$

$$s_{i2} \sim \text{Uniform}(0, B)$$

if the state-space \mathcal{S} is a $B \times B$ square. This homogeneous point process model is customary in most existing applications of SCR models (Royle et al., 2009; Gardner, Royle and Wegan, 2009). We discuss a square \mathcal{S} for simplicity only — any polygon containing \mathbf{x}_r could be used to define the state-space. In practice, it should be chosen large enough so that an individual's encounter rate is negligible if its activity center occurs on the edge of the polygon. This will depend on the specific observation model chosen (see below), and sometimes biological considerations (e.g., suitable habitat) may be used to determine \mathcal{S} (Royle et al., 2009).

3.2. Observation model. It is natural to regard the encounter rate of an individual as a function of the Euclidean distance between the individual's activity center and the trap location, $d_{ir} = \|\mathbf{x}_r - \mathbf{s}_i\|$. To be precise about this, we let z_{irt} be the encounter frequency of individual i in trap r during occasion t . While we will adopt the view that the variables z_{irt} are latent variables (see below), it will be convenient to formulate the model in terms of these variables.

Therefore, we assume that the expected encounter frequency of an individual in some trap is related to d_{ir} as follows:

$$E[z_{irt}] = \lambda_{ir} = \lambda_0 k_{ir}$$

where λ_0 is the expected encounter rate at $d = 0$ and k_{ir} is some positive-valued function of distance d_{ir} . We assume

$$k_{ir} = \exp(-d_{ir}^2/2\sigma^2)$$

where σ is a scale parameter related to home range size. σ also determines the degree of correlation among counts since animals with large home ranges are more likely to be detected at multiple traps relative animals with small home ranges. The phenomenon is analogous to correlation induced by averaging spatial noise, in which case there is a unique correlation between the smoothing kernel and the induced covariance function (Higdon, 2002).

We emphasize that our focus is on situations in which individuals are *not* uniquely identifiable, and therefore the encounter frequencies for each individual cannot be observed, and so they are latent variables. We assume that these latent variables are realizations from a Poisson distribution with mean λ_{ir} :

$$(3.1) \quad z_{irt} \sim \text{Poisson}(\lambda_{ir}).$$

In traditional SCR models, z_{irt} are the observed data, *i.e.*, the frequency of encounters of individual i at trap r on replicate survey t . However, when individual identity is not known, the observed data are the sample- and trap-specific totals, aggregated over all individuals:

$$n_{rt} = \sum_{i=1}^N z_{irt}.$$

Thus the data required by our model are a reduced-information summary of the latent encounter histories.

Under the Poisson encounter model we have that

$$(3.2) \quad n_{rt} \sim \text{Poisson}(\Lambda_r)$$

where

$$\Lambda_r = \lambda_0 \sum_i k_{ir}.$$

Further, because Λ_r does not depend on t , we can aggregate the replicated counts, defining $n_r = \sum_t n_{rt}$ and then

$$n_r \sim \text{Poisson}(T\Lambda_r)$$

As such, T and λ_0 serve equivalent roles as affecting baseline encounter rate. This formulation of the model in terms of the aggregate count simplifies computations as the latent variables z_{irt} do not need to be updated in

the MCMC estimation scheme (see below). However, retaining z_{irt} in the formulation of the model is important if some individuals are uniquely marked, in which case modifying the MCMC algorithm (see below) to include both types of data is trivial. This is because uniquely identifiable individuals produce observations of some of the z_{irt} variables.

We imagine that other observation models might be possible (see Discussion) although we focus here on the Poisson encounter model because it has considerable relevance to animal surveys, and has additional methodological context related to point process models which we address in the Discussion.

Although the model is naturally described conditional on N (i.e., in terms of N latent encounter frequencies z_{irt}), in all practical applications N is unknown and, in fact, is the object of inference. We accommodate that N is unknown using a Bayesian estimation scheme described in the following section.

4. Estimation by MCMC. We adopt a Bayesian framework for inference allowing estimation of N while retaining the formulation of the model that is conditional on the latent activity centers \mathbf{s}_i . Specifically, we employ Markov chain Monte Carlo (MCMC) to simulate posterior distributions of the parameters. However, the fact that N is unknown presents a technical challenge because the size of the parameter space can change with each MC iteration. To resolve this, we adopt the formulation of data augmentation in [Royle, Dorazio and Link \(2007\)](#) who used a specific prior construction for N in terms of individual level Bernoulli trials. In particular, we assume $N \sim \text{Unif}(0, M)$ for some large integer M . We construct this prior by assuming $N|M, \phi \sim \text{Bin}(M, \phi)$ and $\phi \sim \text{DUnif}(0, 1)$ which implies, marginally, that N has the requisite $\text{DUnif}(0, M)$ distribution. However the hierarchical formulation of the prior suggests an implementation in which we introduce a set of latent indicator variables $w_i \sim \text{Bern}(\phi)$ and, furthermore, the model implies that z_{irt} are obtained from the specified distribution (Eq. 3.1) if $w_i = 1$, or if $w_i = 0$, $z_{irt} = 0$ with probability 1. In effect, extending the model in this way induces a reparameterization for the latent counts that is a zero-inflated version of the original conditional-on- N model. Specifically, the model under data augmentation becomes

$$\begin{aligned} z_{irt}|w_i &\sim \text{Poisson}(\lambda_{ir}w_i) \\ w_i &\sim \text{Bern}(\phi) \end{aligned}$$

Under this formulation $N = \sum_{i=1}^M w_i$, and population density is simply $D = N/A(\mathcal{S})$ where $A(\mathcal{S})$ is the area of the point process state-space \mathcal{S} .

We developed two distinct MCMC implementations for this model (Supplement A). In the first, we devised an algorithm for the model conditional on the latent variables z_{irt} . This formulation is useful for problems in which one or more individual identities are available, in which case the z_{irt} are observable for those individuals. The unobserved z_{irt} are easily updated using their full-conditional distribution which is multinomial with sample size n_{rt} . The remaining parameters are updated using Metropolis-Hastings steps (see Supplement A). In the second formulation of the algorithm we applied the Metropolis-Hastings algorithm to the model *unconditional* on the z_{irt} variables. In that case, the marginal distribution for n_{rt} is precisely Eq. 3.2. This algorithm is slightly more convenient because it avoids having to update the z_{irt} variables of which there are many.

5. Applications.

5.1. *Simulation studies.* We carried out two simulation studies to evaluate the basic efficacy of the estimator. In the first study, all individuals were unmarked and we assessed posterior properties under varying degrees of correlation in the counts. In the second study, we measured the improvements in posterior precision obtained by marking a subset of the population.

To investigate the effects of correlation, we used a 15×15 trap grid and simulated scenarios with $\sigma \in (0.5, 0.75, 1.0)$. We selected these values because clearly σ should not be too small relative to the grid spacing or the counts are independent, *i.e.* the trap totals are then just *i.i.d.* Poisson random variables. Similarly, σ should not be too large relative to trap spacing or else again the counts become *i.i.d.* Poisson random variables. We note that trap spacing is widely recognized as being relevant in the application of spatial capture-recapture models, where models require observations of individuals at multiple traps, although to this point in time little formal analysis of the design problem has been done. For the other parameters in the model we considered $T\lambda_0 \in (2.5, 5.0)$ and $N \in (27, 45, 75)$ individuals distributed on a 20×20 unit state-space centered over the 15×15 array of trap locations. This configuration implies a buffer of 3 units around the traps, which was sufficiently large to ensure that encounter rate was negligible for the values of σ considered. We fit the model to 100 datasets for each of the 18 scenarios.

Results of our first simulation study indicate that for the small level of σ , the posterior mode, if regarded as a point estimator of N , is approximately frequentist unbiased (Table 1). However, the posterior distributions are skewed, which results in posterior means exhibiting frequentist bias on the order of 5-10%. Substantial reductions in root-mean-squared error

TABLE 1

Simulation results showing the bias and precision of the posterior mean and mode for the population size parameter, N . Proportion of 95% credible intervals covering the data generating value is also reported. $\lambda_0 = 0.5$ for all cases.

σ	N	T	Mean	RMSE	Mode	RMSE	Coverage
0.50	27	5	30.052	8.683	26.865	6.700	0.940
		10	28.905	5.731	27.168	5.163	0.945
	45	5	50.378	14.503	45.335	11.613	0.930
		10	47.696	9.380	45.223	8.405	0.940
	75	5	85.866	24.735	77.660	19.076	0.940
		10	78.684	14.031	74.705	13.010	0.930
0.75	27	5	30.536	9.511	27.268	7.616	0.880
		10	29.145	5.875	27.425	5.009	0.910
	45	5	54.215	16.963	47.423	12.287	0.923
		10	49.484	12.227	45.783	10.499	0.900
	75	5	82.591	28.556	72.895	22.722	0.930
		10	79.395	19.169	73.125	17.227	0.930
1.00	27	5	33.537	14.767	28.760	11.166	0.910
		10	29.978	8.275	27.473	6.970	0.865
	45	5	58.851	28.692	48.595	22.174	0.880
		10	53.349	17.646	46.540	14.089	0.870
	75	5	87.802	33.919	71.835	31.601	0.940
		10	83.184	24.901	72.205	22.336	0.970

(RMSE) are realized as effective encounter rate doubles from 2.5 to 5.0 ($T=5$ to $T=10$). Coverage is slightly less than nominal for this case. Performance of the estimator deteriorates as σ increases. For $\sigma = 0.75$ the posterior distributions are centered approximately over the data-generating value (having nearly frequentist unbiased modes), but the coverage is quite a bit less than nominal as the posterior becomes more strongly skewed. The general pattern holds for the highest level of $\sigma = 1.0$.

To assess the influence of marking a subset of individuals, we used the same number and configuration of traps as described above, and we set $\sigma = 0.5$, $\lambda_0 = 0.5$, $N = 75$, and $T = 5$. Then, we generated 100 datasets for $m \in (5, 15, 25, 35)$ where m is the number of marked individuals randomly sampled from the population.

Posterior distributions of N for different numbers of marked individuals are shown in Fig. 1. As anticipated, posterior precision increases substantially with the proportion of marked individuals. The posterior mode was approximately unbiased as a point estimator, and the root-mean squared error decreased from 19.076 when all 75 individuals were unmarked to 6.398 when 35 individuals were marked (Tables 1 and 2). Coverage was nominal for all values of m and posterior skew was greatly diminished (Table 2).

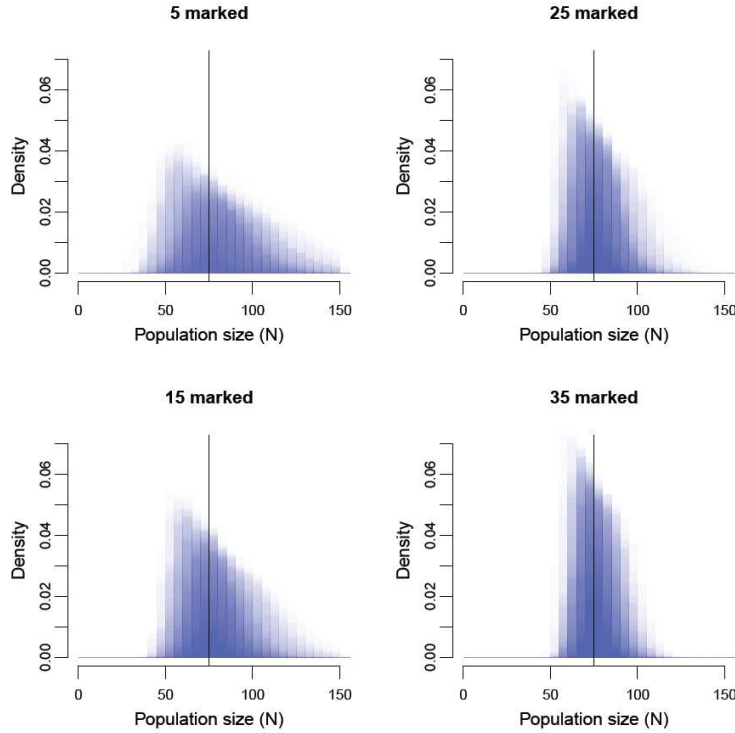


FIG 1. Overlaid posterior distributions of N from 100 simulations for four levels of marked individuals.

5.2. *Point count data.* To apply our model to data collected in the field, we designed a point count study of the northern parula (*Parula americana*), a Neotropical-Nearctic migratory passerine. This species defends well-defined territories during the breeding season (Moldenhauer and Regelski, 1996), and thus our modeling effort was focused on estimating the number and location of territory centers. Points were located on a 50-m grid to ensure spatial correlation. This small grid spacing contrasts with the conventional practice of spacing points by > 200 m to obtain *i.i.d.* counts. Figure 2 depicts the spatially-correlated counts (n_r) from the 105 point count locations surveyed three times each during June 2006 at the Patuxent Wildlife Research Center in Laurel Maryland, USA. A total of 226 detections were made with a maximum count of 4 during a single survey. At 38 points, no warblers were detected. All but one of the detections were of singing males, and this one observation was not included in the analysis.

In our analysis of the parula data, we defined the point process state-space

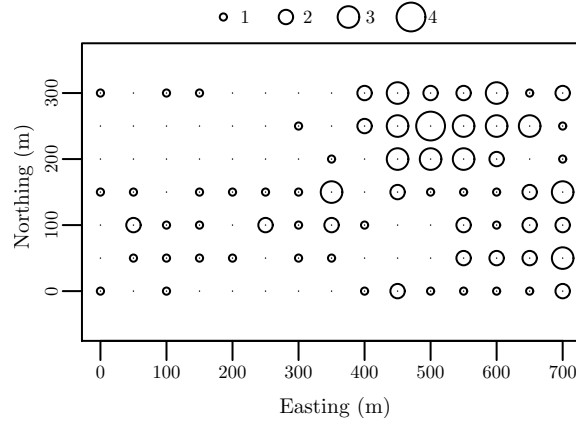


FIG 2. *Spatially-correlated counts of northern parula on a 50-m grid. The size of the circle represents the total number of detections at each point.*

by buffering the grid of point count locations by 250 m and used $M = 300$. We simulated posterior distributions using three Markov chains, each consisting of 300000 iterations after discarding the initial 10000 draws. Convergence was satisfactory, as indicated by an \hat{R} statistic of < 1.02 (Gelman and Rubin, 1992).

One benefit of a Bayesian analysis is that it can accommodate prior information on the home range size and encounter rate parameters, which are readily available for many species. To illustrate, we analyzed the parula data using two sets of priors. In the first set, all priors were improper, customary non-informative priors (see Table 3). Uniform priors were also used in the second set, with the exception of an informative prior for the scale parameter $\sigma \sim \text{Gamma}(13, 10)$. We arrived at this prior using the methods described by Royle, Kéry and Guélat (2011) and published information on the warbler’s home range size and detection probability (Moldenhauer and Regelski, 1996; Simons et al., 2009). More details on this derivation are found in Supplement A. We briefly note here that this prior includes the biologically-

TABLE 2
Posterior mean, mode, and associated RMSE for simulations in which m of $N=75$ individuals were marked. One hundred simulations of each case were conducted.

	Mean	RMSE	Mode	RMSE	Coverage
m=5	80.096	13.948	76.270	13.635	0.980
m=15	78.763	11.548	76.110	10.964	0.940
m=25	77.658	8.826	75.810	8.562	0.950
m=35	76.385	6.453	74.900	6.398	1.000

TABLE 3

Posterior summary statistics for spatial Poisson-count model applied to the northern parula data. Two sets of priors were considered. $M = 300$ was used in both cases.

Parulas/ha, D , is a derived parameter.

Par	Prior	Mean	SD	Mode	q0.025	q0.50	q0.975
σ	$U(0, \infty)$	2.154	1.222	1.230	0.896	1.665	5.170
λ_0	$U(0, \infty)$	0.284	0.149	0.212	0.084	0.256	0.665
N	$U(0, M)$	40.953	38.072	4.000	3.000	31.000	143.000
D	—	0.427	0.397	0.0417	0.0313	0.323	1.490
σ	$G(13, 10)$	1.301	0.258	1.230	0.889	1.266	1.908
λ_0	$U(0, \infty)$	0.298	0.132	0.240	0.098	0.279	0.603
N	$U(0, M)$	59.321	36.489	36.000	18.000	50.000	157.000
D	—	0.618	0.380	0.375	0.188	0.521	1.635

plausible range of values from σ suggested by the published literature.

The posterior distribution for N was highly skewed with a long right tail resulting in a wide 95% credible interval (Table 3). Nonetheless, the interval for density, D , includes estimates reported from more intensive field studies (Moldenhauer and Regelski, 1996). This was true when considering both sets of priors, although posterior precision was higher under the informative set of priors. Specifically, the use of prior information reduced posterior density at high, biologically implausible, values of σ , and hence decreased the posterior mass for low values of N (Fig. 3).

In addition to estimating density, our model can be used to produce density surface maps, which are often used in applied ecological research to direct management efforts and develop hypotheses regarding the factors influencing abundance. Density surface maps can be produced by discretized the state-space and tallying the number of activity centers occurring in each pixel during each MCMC iteration. Parula density was highest near the northeastern corner of the study plot, which may correspond to important habitat features such as suitable nest site locations (Fig. 4). We anticipate future model extensions to directly model the point process intensity using habitat covariates.

6. Discussion. In this paper, we confronted one of the most difficult challenges faced in wildlife sampling — estimation of density in the absence of data to distinguish among individuals. To do so, we developed a novel class of spatially-explicit models that applies to spatially organized counts, where the count locations or devices are located sufficiently close together so that individuals are exposed to encounter at multiple devices. This design yields correlation in the observed counts, and this correlation proves to be informative about encounter probability parameters and hence density. We

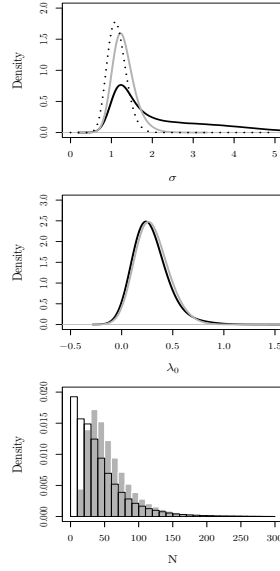


FIG 3. Effects of $\sigma \sim \text{Gamma}(13, 10)$ prior on the posterior distributions from the northern parula model. Posteriors from model with uniform priors are shown in black, and posteriors from the informative prior model are shown in gray. The prior itself is shown as dotted line in the upper panel.

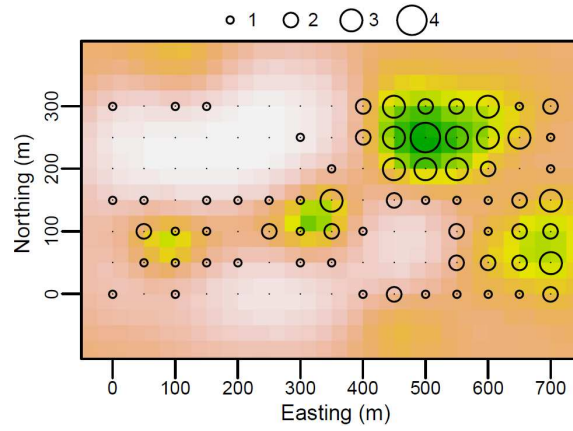


FIG 4. Estimated density surface of northern parula activity centers. The grid of point count locations with count totals is superimposed. See Fig. 1 for additional details.

note that sample locations in count-based studies are typically *not* organized close together in space because conventional wisdom and standard practice dictate that independence of sample units is necessary (Hurlbert, 1984). Our model suggests that in some cases it might be advantageous to deviate from the conventional wisdom if one is interested in direct inference about density. Of course, this is also known in the application of standard spatial capture-recapture models (Borchers and Efford, 2008) where individual identity is preserved across trap encounters, but it is seldom, if ever, considered in the design of more traditional count surveys.

Our model has broad relevance to an incredible number of animal sampling problems. Our motivating problem involved bird point counts where individual identity is typically not available. The model also applies to other standard methods used to sample unmarked populations, such as camera traps or even methods that yield sign (*e.g.* scat, track) counts indexed by space. However, results of our simulation study reveal some important limitations of the basic estimator applied to situations in which none of the individuals can be uniquely identified. In particular, posterior distributions are highly skewed in typical small to moderate sample size situations and posterior precision is low.

Several modifications of the model can lead to improved performance of the estimator. Our simulation results demonstrate that marking a subset of individuals can yield substantial increases in posterior precision. Marking a subset of individuals is commonplace in animal studies such as when a small number of individuals are radio-collared in conjunction with a count-based survey (Bartmann et al., 1987). In many other situations a subset of individuals can be identified by natural marks alone, and thus our model could be applied to data from camera-trapping studies of species such as mountain lions, deer, coyotes for which traditional SCR methods are not effective (Kelly et al., 2008). Thus, the ability to study partially-marked populations adds flexibility to existing SCR methods, and also creates new opportunities for designing efficient SCR studies since the costs of marking all individuals in a population can be prohibitive.

We note the existence of traditional approaches to combining data on marked and unmarked animals based on either the Lincoln-Peterson estimator or so-called “mark-resight” methods. (Bartmann et al., 1987; Minta and Mangel, 1989; McClintock and Hoeting, 2009). In their simplest form, mark-resight methods involve fitting standard closed-population mark-recapture models to the data on marked individuals, and the resultant estimate of detection probability (\hat{p}) is used to estimate population size as $\hat{N} = m + u/\hat{p}$ where m and u are the number of marked and unmarked individual, respectively.

In this case, the unmarked individuals provide no information about the encounter rate parameters, and thus mark-resight methods cannot be used unless a large sample of marked individuals is available. This contrasts with our approach which can be used even when all individuals are unmarked.

In some cases, such as in point counts of birds, it may not be practical to mark individuals. An alternative to increasing posterior precision is to utilize prior information on home range size. Indeed, extensive information on home range size has been compiled for many species in diverse habitats (*e.g.*, DeGraaf and Yamasaki, 2001). It is easy to embody this information in a prior distribution as we demonstrated for the parula data.

An additional design extension that could increase precision is to use multiple sampling methods, in which one method generates encounter frequencies and the other method generates individuality. For example, camera traps are now commonly used with surveys for sign (scat or tracks), or hair snares for sampling bear populations. These distinct methods would have different basal detection rates but share an underlying spatial model describing the organization of individuals in space. Our models show promise for using these disparate data types efficiently for estimating density.

6.1. *N*-mixture models. Parallel developments which appear ostensibly orthogonal to SCR models have addressed the problem of estimating population size when individuals are unmarked. So-called *N*-mixture models (Royle, 2004b,a; Royle, Dawson and Bates, 2004) can be applied to a repeated-measures type of data structure wherein data are collected at R sites, with J replicate surveys are conducted at each. *N*-mixture models regard abundance at each site (N_r) as an *i.i.d.* realization of a discrete distribution such as the Poisson or negative binomial with expectation θ . In the standard binomial *N*-mixture model, the observed counts are treated as binomial outcomes with N_r “trials” and detection probability p .

Although these models have proven useful for studies of factors that affect variation in abundance, interpretation of model parameters is strongly dependent on the assumption that populations are closed with respect to demographic processes and movement. The closure assumption can be an important practical limitation (but see Dail and Madsen, 2011; Chandler, Royle and King, 2011). Furthermore the *i.i.d.* assumption is violated if spatial correlation exists among sites, such as if animals move among plots. Although we formulated the model developed in our paper as an extension of spatially explicit capture-recapture models, it clearly can also be viewed as a spatially explicit extension of *N*-mixture models where the local population sizes N_r are dependent owing to the nature of the sampling design.

Thus, two recently developed methodological frameworks, spatial capture-recapture and N -mixture models, address different problems that arise in sampling animal populations. SCR models address non-closure by accommodating information on the spatial organization of individuals and juxtaposition of individuals with traps, and N -mixture models address inability to uniquely identify individuals. Our model unifies these two modeling frameworks by addressing both issues simultaneously.

6.2. Alternative Observation Models. Several aspects of our “spatial N -mixture model” can be modified to accommodate alternative sampling designs or parametric distributions. We considered situations where an individual can be detected more than once at a trap during a single occasion, but under some designs this is not possible. When collecting DNA samples, for instance, an individual can often be detected at most once during an occasion, because multiple samples of biological material cannot be attributed to distinct episodes. Therefore, rather than $z_{irt} \sim \text{Poisson}(\lambda_{ir})$ we have $z_{irt} \sim \text{Bernoulli}(p_{ir})$ where, for example, $p_{ir} = p_0 \exp(-d_{ir}^2/(2\sigma^2))$, and p_0 is the probability of detecting an individual whose home range is centered on trap r . This Bernoulli model is a focus of ongoing investigations.

Both the Poisson and the Bernoulli models produce count observations when aggregated over individuals to form trap-specific totals; however, ecologists often collect so-called “detection/non-detection” data because it can be easier to determine if “at least one” individual was present rather than enumerating all individuals in a location. In this case, the underlying z_{irt} array is the same as the above cases, but we observe $y_{rt} = I(\sum_{i=1}^N z_{irt} > 0)$ where I is the indicator function. This “Poisson-binary model” is a spatially explicit extension of the model of [Royle and Nichols \(2003\)](#) in which the underlying abundance state is inferred from binary data. We have investigated this model to a limited extent but do not report on those results here.

6.3. Spatial point process models. Our model has some direct linkages to existing point process models. We note that the observation intensity function (i.e., corresponding to the observation locations) is a compound Gaussian kernel similar to that of the Thomas process ([Thomas, 1949](#); [Møller and Waagepetersen, 2003](#), pp. 61-62). Also, the Poisson-Gamma Convolution models ([Wolpert and Ickstadt, 1998](#)) are structurally similar (see also [Higdon \(1998\)](#) and [Best, Ickstadt and Wolpert \(2000\)](#)). In particular, our model is such a model but with a *constant* basal encounter rate λ_0 and *unknown* number and location of “support points”, which in our case are the animal activity centers, \mathbf{s}_i . We can thus regard our model as a model for *estimating* the location and local density of support points in such models,

which we believe could be useful in the application of convolution models. [Best, Ickstadt and Wolpert \(2000\)](#) devise an MCMC algorithm for the Poisson-Gamma model based on data augmentation, which is similar to the component of our algorithm for updating the z variables in the conditional-on- z formulation of the model. We emphasize that our model is distinct from these Poisson-Gamma models in that the number *and* location of such support points are estimated.

If individuals were perfectly observable then the resulting point process of locations is clearly a standard Poisson or Binomial (fixed N) cluster process or Neyman-Scott process. If detection is uniform over space but imperfect, then the basic process is unaffected by this random thinning. Our model can therefore be viewed formally as a Poisson (or Binomial) cluster process model but one in which the thinning is non-uniform, governed by the encounter model which dictates that thinning rate increases with distance from the observation points. In addition, our inference objective is, essentially, to estimate the number of parents in the underlying Poisson cluster process, where the observations are biased by an incomplete sampling apparatus (points in space).

As a model of a thinned point process, our model has much in common with classical distance sampling models ([Buckland et al., 2001](#)). The main distinction is that our data structure does *not* include observed distances, although the underlying observation model is fundamentally the same as in distance sampling if there is only a single replicate sample and \mathbf{s}_i is defined as an individual’s location at an instant in time. For replicate samples, our model preserves (latent) individuality across samples and traps which is not a feature of distance sampling. We note that error in measurement of distance is not a relevant consideration in our model, and we explicitly do not require the standard distance sampling assumption that the probability of detection is 1 if an individual occurs at the survey point. More importantly, distance sampling models cannot be applied to data from many of the sampling designs for which our model is relevant. For example, many rare and endangered species can only be effectively surveyed using methods such as hair snares and camera traps that do not produce distance data ([O’Connell, Nichols and Karanth, 2010](#)).

7. Conclusion. Concerns about “statistical independence” have prompted ecologists to design count-based studies such that observed random variables can be regarded as *i.i.d.* outcomes ([Hurlbert, 1984](#)). Interestingly, this often proves impossible in practice, and elaborate methods have been devised to model spatial dependence as a nuisance parameter. Our paper presents a

modeling framework that directly confronts this view by demonstrating that spatial correlation carries information about the locations of individuals, which can be used to estimate density even when individuals are unmarked and distance-related heterogeneity exists in encounter probability.

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SUPPLEMENTARY MATERIAL

Supplement A: R code and parula dataset

(<http://lib.stat.cmu.edu/aoas/???/???>). Includes MCMC algorithms, data simulator, northern parula dataset, and a description of method used to obtain the informative prior used in the analysis of the parula data.

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